Maintaining distances with the engineer: patterns of coexistence in plant communities beyond the patch-bare dichotomy

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Summary

- Two-phase plant communities with an engineer conforming conspicuous patches and affecting the performance and patterns of coexisting species are the norm under stressful conditions.
- To unveil the mechanisms governing coexistence in these communities at multiple spatial scales, we have developed a new point-raster approach of spatial pattern analysis, which was applied to a Mediterranean high mountain grassland to show how *Festuca curvifolia* patches affect the local distribution of coexisting species.
- We recorded 22 111 individuals of 17 plant perennial species. Most coexisting species were negatively associated with *F. curvifolia* clumps. Nevertheless, bivariate nearest-neighbor analyses revealed that the majority of coexisting species were confined at relatively short distances from *F. curvifolia* borders (between 0–2 cm and up to 8 cm in some cases).
- Our study suggests the existence of a fine-scale effect of *F. curvifolia* for most species promoting coexistence through a mechanism we call 'facilitation in the halo'. Most coexisting species are displaced to an interphase area between patches, where two opposite forces reach equilibrium: attenuated severe conditions by proximity to the *F. curvifolia* canopy (nutrient-rich islands) and competitive exclusion mitigated by avoiding direct contact with *F. curvifolia*.

Introduction

Two-phase plant community patterns with plants grouped in conspicuous patches on a bare ground matrix is the norm in harsh habitats (Wiens, 1976). These patterns can vary from stripes and arcs to spotted clumps of plants as a function of slope anisotropy (Deblauwe *et al.*, 2011). Previous studies have attributed pattern formation to abiotic processes related to water reallocation through runoff and infiltration in arid regions (Ludwig *et al.*, 2005; Puigdefábregas, 2005), and to topography or other external agents, such as soil particle size (Cox & Larson, 1993; Pérez, 2012), differential soil resource distribution (Kershaw, 1963), unidirectional wind (Okin & Gillette, 2001) or cryoturbation and solifluxion in arctic and alpine ecosystems (Liptzin, 2006). Vegetated patches in alpine ecosystems are usually dominated by one or few species with graminoid or cushion-like habits (Körner, 2003), while patches in arid regions are usually dominated by shrubs, which act as genuine ecosystem engineers affecting the ecosystem as a whole (Jones *et al.*, 1994; Badano *et al.*, 2006). Furthermore, some demographic processes of these dominant species –frequently just one – determine both the construction and the degenerative stage of the clumped structure and result in 'patch dynamics' (Aguiar & Sala, 1999).

The existence of two-phase structures has a great effect on critical ecosystem processes, such as water dynamics and nutrient cycling, and on the direction and intensity of biotic interactions that plants establish with their neighbors (Theodose & Bowman, 1997). Vegetation clumps are the result of intrinsic self-organized mechanisms related to the performance of dominant species (Lejeune *et al.*, 1999), where feedbacks between biomass (above–below-ground relationships) and water (Gilad *et al.*, 2004; Meron, 2012) can be controlled by plant–plant interactions. In particular, concepts such as islands of fertility (Burke *et al.*, 1998) or nurse plants (Callaway & Walker, 1997) were proposed, and a new paradigm in which facilitation is prevalent in stressful habitats emerged (Callaway *et al.*, 2002; Bruno *et al.*, 2003; Brooker *et al.*, 2008). The effect of patchy structures on diversity has also been explored, including its functional (Schöb *et al.*, 2012) and phylogenetic components (Valiente-Banuet *et al.*, 2006; Butterfield *et al.*, 2013) at different spatial scales (Cavieres *et al.*, 2014).

Previous studies on two-phase communities in alpine environments have generally found that the main engineers in the community exert a positive (i.e. facilitative) effect (Badano & Cavieres, 2006; Cavieres *et al.*, 2014; but see, de Bello *et al.*, 2011; Dvorský *et al.*, 2013). Most of these studies base their conclusions on positive associations detected between plants at some predetermined spatial scale (usually the scale of the vegetated patch), which is usually interpreted to be the result of positive interactions. However, by only focusing on a predetermined scale, this approach does not detect other possible causes of positive associations, such as the existence of shared microhabitat linked to heterogeneous resource distribution (Seabloom *et al.*,

2005). Environmental heterogeneity is known to affect the spatial distribution of organisms and can confound the detection of positive and negative associations between them (Getzin *et al.*, 2008). On the other hand, association or repulsion between species can be mediated by specific attributes such as plant size (Yeaton *et al.*, 1977; Phillips & MacMahon, 1981), life-history strategies (Michalet, 2007), and functional attributes (Schöb *et al.*, 2012), which could condition the scale at which positive or negative associations occur. All this makes the use of just one spatial scale unsatisfactory if we want to gain an insight ino how and why diversity is structured at different scales in these communities. In other words, we can only separate the first- and second-order spatial effects on realized patterns by simultaneously considering a wide array of scales using appropriate techniques.

We are witnessing an explosion of studies using spatial statistics in ecology (Wiegand & Moloney, 2004; Perry *et al.*, 2006; Law *et al.*, 2009; Wang *et al.*, 2011; Lan *et al.*, 2012). Spatial point pattern analysis can help to infer the ecological mechanisms underlying the spatial structures within the community (Mcintire & Fajardo, 2009; Brown *et al.*, 2011). These methods are especially suited to detecting the spatial scales at which ecological processes are operating (i.e. those linked to environmental heterogeneity (Getzin *et al.*, 2008; Shen *et al.*, 2013) and to plant interactions and dispersal (Amarasekare, 2003; Wiegand *et al.*, 2009)). A panoply of analyses are routinely used to evaluate spatial patterns and their underlying mechanisms (Wiegand *et al.*, 2013) by considering each plant as a discrete point in space (Ripley, 1981; Stoyan & Stoyan, 1994; Diggle, 2003). However, when the shape or size of the plant is relevant, a point pattern perspective may not be efficient in exploring spatial plant relationships at fine scales (Nuske *et al.*, 2009). In fact, the point assumption is only reasonable if the area of events is small relative to the spacing between them (Dixon, 2006). We are aware of only one study in which these techniques have been employed, the one conducted by Fajardo *et al.* (2008). These authors recognized the misuse of the point assumptions. However, there are other alternatives such as the so-called 'raster approach' (Wiegand *et al.*, 2006), which was developed for cases where individuals are better represented by shapes than by points. In this study, we propose the use of a point-raster approach as an intermediate approach between the usual point pattern and the raster approach. In this case, individuals of the dominating species forming the patch are represented by a grid of points delineating their real shape, whereas the individuals of the accompanying species are represented by single points. This is convenient, as the individuals of dominant species are more than one order of magnitude larger than the other species. This allows us to use spatial point pattern techniques and solves the problem of the extensive individuals of the engineer plant.

Other neglected point pattern techniques, such as Berman's test (Berman, 1986) and point process modeling (Baddeley & Turner, 2000), can still help to determine the factors conditioning the spatial distribution of species within the community and distinguish heterogeneity from plant interactions and dispersal.

With this in mind, we studied a pasture-like alpine Mediterranean community above the treeline. This type of community is a good example of a patched community in which spots and stripes are perpendicular to the slopes as a result of environmental severity. These patches are formed by clumps of the perennial graminoid, *Festuca curvifolia*, together with more than 20 perennial specialists interspersed within the clumps or directly in the ground terraces between stripes. We mapped a well-conserved area in this community in Sierra de Guadarrama in central Spain. We asked whether the presence of *F. curvifolia* patches is affected the distribution of the other perennial species in the community and at which spatial scales this occurs. As we expected the pattern of each perennial species in the community to be facilitated by the presence and abundance of this grass (Cavieres *et al.*, 2006), we specifically tested whether the occurrence of each perennial within or outside the clumps is more or less frequent than expected by chance; the existence and range of short-scale attraction or repulsion; and whether *F. curvifolia* is responsible for the heterogeneous distribution of the other perennial species in the study community.

Materials and Methods

Study site and sampling

This study was conducted in a Mediterranean high mountain grassland located in the Sierra de Guadarrama National Park in the center of Spain. The climate in this region is Mediterranean with a mean annual temperature of 6.4°C and a mean annual precipitation of 1350 mm, with an intense summer drought (Navacerrada Pass weather station; 40°47′N, 4°0′W; 1894 m above sea level (a.s.l.)). This community extends far above the timberline, which is located between 1900 and 2000 m a.s.l. and is dominated by Scots pines (*Pinus sylvestris* L.) interspersed in a shrubby-pasture matrix dominated by *Cytisus oromediterraneus* Rivas Mart *et al.* and *Juniperus communis* L. ssp. *alpina* (Suter) Čelak. The vegetation in these alpine *islands* is organized in a two-phase structure dominated by *Festuca curvifolia* Lag. *ex* Lange. This perennial graminoid represents the main structural and cover element in this community, forming small ellipsoid-shaped patches and stripes, which do not normally exceed 30 cm in length, in a bare ground matrix (Supporting Information, Figs S1, S2). The community also includes several local endemisms, such as *Jasione crispa* (Pourr.) Samp., *Pilosella vahlii* (Froel.) F.W. Schultz & Sch. Bip., *Minuartia recurva* (All.) Schinz & Thell., *Armeria caespitosa* (Gómez Ortega) Boiss. in DC. or *Erysimum penyalarense* (Pau) Polatschek together with arctic-alpine elements, such as *Agrostis rupestris* (All.), which reach their latitudinal southernmost limit here.

In the summer of 2012, we established a rectangular 9 × 6 m plot (40°47′10″N, 3°58′51″W; 2210 m a.s.l.) in a homogenous and representative area of this community. The community was fully mapped and plant sizes were recorded by drawing the outline of each perennial plant on transparent DIN-A3 sheets of polyvinyl chloride (PVC), which were supported in a mobile methacrylate structure suspended 5 cm over the soil surface. In the case of clonal species, we drew the outline of each independent clump and considered each clump to be an independent individual. We performed cross-slope transects with this system

throughout the entire plot area. Finally, we recorded 30 random X–Y coordinates in the plot with a GPS Leica Viva GS15 system to georeference the sheet mosaic with a precision below 2 cm.

Digitalization and layer compilation

A total of 420 PVC sheets were recorded and converted to digital images with a photo-scanner (Epson Expression 10000XL, Seiko Epson Corp., Nagano, Japan). All images were assembled in a unique picture with Adobe Photoshop CS3 software (Adobe Systems, San Jose, CA, USA) and compressed to jpeg format. The image was georeferenced to the projection UTM 30N–ETRS89 using the 30 random X–Y coordinates. Each individual plant recorded was then digitalized in ArcGIS 10.1 software (ESRI, 2011) with the help of the interactive pen display Wacom DTU-2231 (Vancouver, WA, USA). First, we obtained a vector layer for each species with a polygon for each individual. We then measured the total area, perimeter, maximum and minimum axes (length and width) and centroids (plant center) of each polygon (i.e. individual). Using the vector layer for *F. curvifolia*, we built two types of map. We first built a raster map with a cell size of 5 cm representing the percentage cover of *F. curvifolia* per cell. Secondly, we built a map transforming *F. curvifolia* polygons into masses of points, that is, each polygon was converted into a grid of points (separated by 0.5 cm in accordance with the smallest *F. curvifolia* clump) which accurately preserved clump size and shape. This map was created with ArcGis 10.1 software (ESRI, 2011).

Statistical analysis

To test the role of the dominant plant species, we focused on the influence of *F. curvifolia* at two scales. The first scale was a fine scale at which the observed patterns were generated by direct plant–plant interactions. This scale was examined using the classical contingency table approach for biphasic communities, which considers space as a template in which two alternative stages are possible (i.e. bare ground or *F. curvifolia* clumps). We also used a new point pattern analysis technique (distribution function of nearest-neighbor distances between points of plants and masses of points resembling *F. curvifolia* individuals). The second scale was a coarse scale at which we evaluated the role of *F. curvifolia* cover as a driver of first-order heterogeneity of coexisting species patterns, as well as distribution and local density of each species.

Contingency table approach We analyzed if there was a pairwise association between *F. curvifolia* clumps and the 10 most abundant species in the community (i.e. species with more than 100 individuals; hereafter coexisting species). We tested whether the occurrence of each coexisting species in *F. curvifolia* clumps and in the bare ground was greater or lower than expected by chance. For this, we built a contingency table for each coexisting species with the observed numbers of individuals that appeared inside and outside *F. curvifolia* patches and the expected numbers under the assumption of independence (i.e. dividing the total number of individuals among the inside and outside classes in proportion to the surface area occupied by *F. curvifolia* clumps and bare soil, respectively). We computed a Fisher's exact test for each species' contingency table.

Small-scale association between *F. curvifolia* clumps and the coexisting species To evaluate the small-scale association between *F. curvifolia* clumps and the coexisting species, we computed the so-called (bivariate) nearest-neighbor distance function distribution ($G_{ij}(x)$; Diggle, 2003), that is, the cumulative distribution function of the distance from each coexisting species to the nearest *F. curvifolia* individual. As *F. curvifolia* clumps are considerably larger than the individuals of coexisting species, we approximated these individuals to a point using their centroids, whereas *F. curvifolia* clumps were considered with the 0.5 cm masses of points. This point-raster approach, an intermediate approach between classical point pattern techniques and those of Wiegand *et al.* (2006) and Nuske *et al.* (2009) for extensive individuals, allows the accurate estimation of nearest-neighbor relationships between objects of different types (points and shapes). On the other hand, representing the accompanying species as points allows the use of the toolset of point process modeling for model fitting and inference. Besides, individual centroids usually coincide with the rooting point (i.e. the establishment point), and we can then explore the effects of patches on species establishment.

Traditionally, inference for bivariate point pattern analysis has relied on the well- known method of toroidal shift (Goreaud & Pélissier, 2003). This is inadequate when individual patterns are not stationary. Instead, we tested G_{ij} functions computing the usual Monte Carlo envelopes simulating each accompanying species from an appropriate null model; that is, a model which describes the small- and large-scale properties of the realized patterns (Wiegand & Moloney, 2004). To select the appropriate null model for each coexisting species, we followed an approach conceptually similar to the pattern reconstruction strategy of Wiegand *et al.* (2013).We first fitted a battery of different spatial models for each species: (1) a homogeneous Poisson process with constant intensity λ equal to the density of the observed pattern; (2) a homogeneous Poisson cluster process with constant intensity λ and parameters σ and ρ fitted by minimum contrast (Diggle, 2003); (3) 16 heterogeneous Poisson processes with an intensity function $\lambda(x,y)$ estimated with a Gaussian kernel (Wiegand *et al.*, 2007) with 16 different σ values to experiment different bandwidths from $\sigma = 0.5$ to $\sigma = 2.0$ m; and, finally, 16 heterogeneous Poisson cluster processes (Waagepetersen, 2007) with parameters σ and ρ fitted by minimum contrast and intensity functions estimated as in (3). We then evaluated their overall fit with the goodness-of-fit u statistic (Diggle, 2003; Loosmore & Ford, 2006),

$$u = \int_{r=0}^{r_{max}} \{\hat{K}(r) - \bar{K}(r)\}^2 dr \qquad \text{Eqn 1}$$

where $\hat{K}(r)$ is the estimation of Ripley's K-function (Ripley, 1977) for each coexisting species, $\bar{K}(r)$ is the mean of the K functions of 199 patterns simulated according to the evaluated null model, and r is the range of spatial scales at which the functions are estimated. We estimated the K functions with r up to 150 cm with 1 cm lags. After adjusting and evaluating all the mentioned

models, we selected the model that produced the smallest u value as the 'appropriate' model for each species. When evaluating heterogeneous models, we substituted the inhomogeneous K function (Baddeley *et al.*, 2000) for K in the calculation of u.

Inferences about the association between each coexisting species and *F. curvifolia* clumps were obtained by comparing the empirical G_{ij} function with the fifth-lowest and fifth-highest values of 199 G_{ij} functions computed keeping the *F. curvifolia* grid of points 'fixed' and simulating the distributions of each species' individuals obtained by the appropriate null model. For each envelope test, we computed a goodness-of-fit test (Diggle, 2003; Loosmore & Ford, 2006; Baddeley *et al.*, 2014) in the range where there were apparent significant differences (i.e. when the observed pattern remained outside the envelopes built under the null model).

Large-scale effects driven by *F. curvifolia* cover on coexisting species patterns We first analyzed the association between the spatial distribution of each coexisting species and *F. curvifolia* clumps by computing the Z1 statistic of Berman (1986). This statistic tests the association between a point pattern and a covariate. It is defined as $Z1 = (S - \mu)/\sigma$, where S is the sum of the values of the covariate at each data point, and μ and σ are the mean and standard deviation of the values of the covariate in the study area, respectively. Under the null hypothesis of no association, $Z1$ would have a standard normal distribution. As covariates we used a raster map with 5 cm resolution summarizing the percentage cover of *F. curvifolia* and another raster map with a 1 cm resolution with the distance from each pixel to the nearest *F. curvifolia* clump.

Finally, we explored whether *F. curvifolia* clumps had significant effects on the large-scale spatial pattern (i.e. in the first-order heterogeneity) of the coexisting species. For this, we fitted heterogeneous Poisson processes to each species, assuming that the intensity function $\lambda(x)$ was dependent on *F. curvifolia* cover. Thus, we employed the ppm() function of spatstat (Baddeley & Turner, 2005), which fits the intensity of the observed point pattern as a log-linear function of one or several covariates maximizing likelihood (Baddeley & Turner, 2000). As covariates, we used several versions of the *F. curvifolia* cover map (at 1, 5, 10, 20, and 50 cm pixel resolutions).We fitted intensity surfaces to each of these *F. curvifolia* maps for each species. These surfaces were used to compute the inhomogeneous K function (Baddeley *et al.*, 2000) and to simulate heterogeneous Poisson patterns (HPPs) as a basis for testing whether the fitted intensity surfaces accounted for the heterogeneity of each species. For this, we compared the empirical inhomogeneous L function $\left[L(r) = \sqrt{\frac{K(r)}{\pi}} - r\right]$ with the fifth-lowest and fifth-highest values of 199 simulations of the fitted HPP processes. If the inhomogeneous L function remained inside the envelopes at large spatial scales, we concluded that the model explained the heterogeneous pattern of the tested coexisting species.

All statistical analyses were conducted in R version 3.0.2 (R Core Team, 2012) using the packages spatstat (Baddeley & Turner, 2005) and ecespa (De la Cruz, 2008).

Results

We recorded a total of 22 111 individuals of 17 perennial plant species, of which *F. curvifolia* was the most abundant (Table 1). The bare ground fraction occupied 67.84% of the plot, and *F. curvifolia* dominated the vegetation fraction with a cover of 26.19% (Table 1). *F. curvifolia* individuals had a mean size of 12.67 cm^2, with 25% of individuals being smaller than 1 cm^2 and 75% not exceeding 6.35 cm^2. The largest *F. curvifolia* individual reached 3405 cm^2. Mean nearest-neighbor distance between *F. curvifolia* individuals was 1.03 cm ($\pm$ 0.87), and the greatest distance was 8.48 cm.

Contingency table analyses showed that all coexisting species except *E. penyalarense* and *J. crispa* were negatively associated with *F. curvifolia* (Table 2). This suggests that most species tended to appear more frequently outside *F. curvifolia* clumps.

Bivariate nearest-neighbor distance results showed that *J. crispa* and *E. penyalarense* tended to appear close to borders of *F. curvifolia* individuals more frequently than expected (at distances between 1 and 6.7 cm and between 0.6 and 6.2 cm, respectively; Fig. 1). However, *F. curvifolia* exerted an inhibitory effect on most species at short distances (*c.* between 0 and 2 cm) or medium distances (> 8 cm in the case of *A. delicatula* and *M. recurva*). On the other hand, *A. caespitosa* and *J. humilis* showed preference to have its nearest *F. curvifolia* between 3.5 and 6.7 cm and between 2.6 and 8.4 cm, respectively (Fig. 1).

Berman's tests revealed that the spatial pattern of most coexisting species was significantly associated with both *F. curvifolia* cover and distance to the nearest *F. curvifolia* individual (Table 2). The sign of this association varied depending on the species and the covariate. Specifically, *E. penyalarense* and *J. crispa* were significantly and negatively associated with distance to *F. curvifolia* (Table 2). *E. penyalarense* was the only species that was positively associated with *F. curvifolia* cover, while the association between this covariate and most species was significantly negative (Table 2). It is noteworthy that only a few species were not significantly affected by *F. curvifolia* cover (e.g. *Sedum* species) or distance (*Jurinea humilis*).

All coexisting species showed heterogeneous patterns (Table S1). In all cases, the best models included intensity surfaces estimated from their own pattern with Gaussian kernels. None of the heterogeneous Poisson models fitted to *F. curvifolia* cover accounted for the heterogeneity of any of the coexisting species (Fig. S3).

Discussion

Applying emergent coexistence paradigms (Götzenberger *et al.*, 2012; HilleRisLambers *et al.*, 2012) to two-phase plant communities dominated by a single species is a challenge for which current statistical tools are clearly inappropriate (Wiegand *et al.*, 2006). Our Mediterranean high mountain community constitutes a good example of these communities in which *F. curvifolia*, a graminoid with stripe-clonal growth, represents a genuine ecosystem engineer (Jones *et al.*, 1994). Its spatial distribution and cover (small patches close to larger ones and a cover one order of magnitude

Table 1 Descriptive statistics of the species present in the Guadarrama plot

Species	Individuals observed	Individuals observed inside *F. curvifolia* clumps	Distance to *F. curvifolia* (mean ± SD, cm)	Maximum individual diameter (mean ± SD, cm)	Total area (m^2)	Percentage cover (%)
Agrostis delicatula Pourr. ex Lapeyr.	1072	35	2.14 ± 1.65	1.69 ± 0.89	0.18	0.37
Armeria caespitosa (Gómez Ortega) Boiss. in DC.	2841	256	1.56 ± 1.41	1.16 ± 0.58	0.27	0.55
Biscutella valentina ssp. *pyrenaica* (A. Huet) Grau & Klingenberg	1	0	1.08	4.43	7.05×10^{-4}	<0.01
Deschampsia flexuosa (L.) Trin.	13	0	1.71 ± 0.72	3.13 ± 2.68	8.83×10^{-3}	0.02
Erysimum penyalarense (Pau) Polatschek.	486	140	0.92 ± 1.22	1.07 ± 0.43	4.1×10^{-2}	0.08
Festuca curvifolia Lag. ex Lange	10035	–	–	3.8 ± 5.42	12.71	26.19
Jasione crispa (Pourr.) Samp.	906	203	1.18 ± 1.34	4.7 ± 2.81	0.79	1.63
Juniperus communis ssp. *alpina* (Suter) Čelak	7	2	1.56 ± 1.22	8.06 ± 5.94	2.29×10^{-2}	0.05
Jurinea humilis (Desf.) DC.	1989	317	1.47 ± 1.37	2.51 ± 1.3	0.47	0.97
Luzula hispanica Chrtek & Krísa	14	1	2.59 ± 1.96	3.07 ± 1.25	8.12×10^{-3}	0.02
Minuartia recurva (All.) Schinz & Thell	219	36	1.73 ± 1.84	3.68 ± 2.38	0.19	0.39
Pilosella vahlii (Froel.) F.W. Schultz & Sch. Bip.	3568	368	1.68 ± 1.49	1.9 ± 0.76	0.59	1.21
Rumex acetosella L.	55	3	1.43 ± 1.22	0.81 ± 0.33	1.74×10^{-3}	<0.01
Sedum brevifolium DC.	455	46	1.57 ± 1.57	0.84 ± 0.65	2.34×10^{-2}	0.05
Sedum candollei Raym.-Hamet	152	5	1.78 ± 1.52	0.74 ± 0.19	5.64×10^{-3}	0.01
Senecio carpetanus Boiss & Reuter	7	0	1.23 ± 0.56	3.05 ± 2.09	3.03×10^{-3}	0.01
Silene ciliata Pourr.	291	39	1.89 ± 1.59	4.02 ± 2.49	0.29	0.60
Total	22111	1451	1.59 ± 1.48	2.83 ± 3.94	15.60	32.15

Species in bold (> 100 individuals in the plot) represent the coexisting species of *F. curvifolia* considered in all statistical analyses. Nomenclature of species and subspecies was standardized according to Flora Iberica (Castroviejo, 1986–2012; http://www.floraiberica.org/; 28 October 2013).

greater than all of the other species together) conform to a complex structure of patch and bare structures affecting the distribution of available resources to other species.

In a previous study in this ecosystem following a contingency table approach, Gavilán *et al.* (2002) also found that *F. curvifolia* does not appear to be associated with other species. Furthermore, in our study, only two species, *E. penyalarense* and *J. crispa*, showed no preference for either of these two habitats (bare ground or graminoid clumps), while the other coexisting species had a negative association to *F. curvifolia*. The results for most species were concurrent with those from our Berman's test analyses. However, the spatial structure of the two 'indifferent' species had a negative value of Z1 for distance to *F. curvifolia* patches. This means that they appeared closer to graminoid clumps than would be expected by chance. *E. penyalarense* was also positively associated with areas of high *F. curvifolia* cover. In other words, when considering the spatial organization of the community, they may not be so indifferent. Most of the remaining species showed a significant positive association with distance to *F. curvifolia*, and were negatively associated with *F. curvifolia* cover, suggesting competitive exclusion. Nevertheless, the balance between facilitation and competition in stressed environments seems to be a dynamic process (Callaway & Walker, 1997), with interactions varying as a function of shifting abiotic factors in space–time (Holmgren *et al.*, 1997), life stages of the protagonists (Miriti, 2006; Soliveres *et al.*, 2010) or shifts induced by dynamic and spatial organization (Bolker *et al.*, 2003; Meron, 2012). The analyses of the distribution of crossed nearest-neighbor distances provide an insight into the processes that may be structuring this community. For most coexisting species, *F. curvifolia* patches seem to produce an exclusion pattern at very short distances (from 0 to 2 cm), except in the case of *A. delicatula* where this distance is over 8 cm (Fig. 1). For other species, *F. curvifolia* patches seem to exert attraction at short and medium distances (i.e. *E. penyalarense*, *J. crispa*, *A. caespitosa*, and *J. humilis*). The exclusion pattern at short distances suggests that our engineer species produces a repulsion halo adjacent to their clump borders. Previous studies have reported the presence of this competition halo around *Hieracium pilosella* (Boswell & Espie, 1998) and in *Stipa tenacissima* tussocks (Armas & Pugnaire, 2011), primarily as a result of competition for water. Summer drought stress is a proven fact in Mediterranean high mountain (Cavieres *et al.*, 2006; Giménez-Benavides *et al.*, 2007; Schöb *et al.*, 2013), although water is not a limiting resource in the rest of alpine ecosystems (Körner, 2003). This water limitation is

Table 2 Results of Fisher's exact test and Berman's test for each coexisting species

	Fisher's exact test		Berman distance		Berman cover	
Species	Odds ratio	*P*-value	Z1	*P*-value	Z1	*P*-value
Agrostis delicatula	0.10	**< 0.001**	11.06	**< 0.001**	−7.95	**< 0.001**
Armeria caespitosa	0.28	**< 0.001**	3.93	**< 0.001**	−9.28	**< 0.001**
Erysimum penyalarense	1.14	0.38	−4.92	**< 0.001**	4.34	**< 0.001**
Jasione crispa	0.82	0.07	−3.18	**0.001**	−0.91	0.362
Jurinea humilis	0.53	**< 0.001**	1.16	0.247	−0.70	0.482
Minuartia recurva	0.56	**0.02**	2.11	**0.035**	−2.19	**0.028**
Pilosella vahlii	0.32	**< 0.001**	6.81	**< 0.001**	−8.38	**< 0.001**
Sedum brevifolium	0.32	**< 0.001**	1.98	**0.048**	−0.57	0.570
Sedum candollei	0.10	**< 0.001**	2.27	**0.023**	−1.27	0.206
Silene ciliata	0.44	**< 0.001**	3.94	**< 0.001**	−2.96	**0.003**

Fisher's exact test results (odds ratio and *P*-value) evaluate the significance of a contingency table with expected and observed individuals of each species found inside and outside *Festuca curvifolia* clumps. Berman's test performed a goodness-of-fit test of the Poisson point process model for each coexisting species' point pattern dataset. The value of each covariate (distance to *F. curvifolia* and *F. curvifolia* cover) is evaluated at the coexisting species points and its sum is compared with their expected value according to the distribution of covariate values in the whole plot. Significant results are in bold.

probably exacerbated in the thin, sandy-textured soils where our *F. curvifolia* grasslands occur.

Despite the conspicuous patch-bare dichotomy, the robust associations between *F. curvifolia* and most coexisting species at this halo indicate that the influence of *F. curvifolia* clumps on the distribution of the species in the community extends beyond their canopy. The realized patterns of most species being negatively associated with *F. curvifolia*, but confined to short and medium distances around its borders, suggests the existence of a sort of variable facilitation signature. This may result from the behavior of *F. curvifolia* roots, which may act as a 'nutrient pump' (Richards & Caldwell, 1987), capturing soil resources. Furthermore, the above-ground biomass of *F. curvifolia* may act as a carpet, trapping both nutrients and water from overflow, precipitation and/or wind (Coppinger *et al.*, 1991; Ehrenfeld *et al.*, 2005). This mechanism, referred to as an 'island of fertility', ameliorates conditions within patches and in adjacent areas. Previous studies carried out in several localities of Sierra de Guadarrama (Escudero *et al.*, 2004; D. S. Pescador & A. Escudero, unpublished) showed that soils below *F. curvifolia* patches are richer in nutrients than soils below bare ground (e.g. 4.5 ± 1.8 mg of total N g^{-1} soil below *F. curvifolia* vs 3.7 ± 1.4 mg of total N g^{-1} bare ground soil or $5.9 \pm 2.4\%$ of organic carbon in soil below *F. curvifolia* vs $4.3 \pm 1.6\%$ of organic carbon in bare ground soils). *F. curvifolia* is also scarcely palatable for sheep, cows, or goats because of its foliar toughness and acicularity, providing secure anti-grazing sites for coexisting species (Gavilán *et al.*, 2002) and for their seeds, which may be easily trapped and facilitated (Haussmann *et al.*, 2010). The positive effects exerted by *F. curvifolia* and its resource island may become negative in the close proximity of *F. curvifolia* and within clumps, because of *F. curvifolia*'s dense root system and above-ground biomass. This suggests that *F. curvifolia* competes for resources (i.e. water, nutrient, and light) more efficiently than the coexisting species in the community. In summary, the facilitative effect is compensated by the strong competitive ability of the engineer (Fig. 2) and the net effect would result from the balance between positive and negative interactions and also between above- and below-ground biomass. Plants probably benefit from the resources accumulated under *F. curvifolia* but avoid direct competition with its canopy. Consequently, most coexisting species find themselves displaced to a security ring or interphase habitat around clumps, where environmental conditions are not as stressful as in the bare zone or as competitive as within *F. curvifolia* patches. This displacement is especially apparent in the case of *A. delicatula*, a graminoid relative of *F. curvifolia*. These two species share many functional, especially ecophysiological, traits, which could make competition more intense (Cavender-Bares *et al.*, 2004; Valiente-Banuet & Verdú, 2008). To support these findings, we examined the relationship between the individual size (i.e. maximum individual diameter) of each coexisting species and distance to the nearest *F. curvifolia* individual. Several coexisting species (i.e. *A. caespitosa*, *J. crispa*, *J. humilis*, and *P. vahlii*) had a significant negative relationship (Table S2), suggesting a prevalence of this mechanism at short distances. In case of *A. delicatula*, we detected the opposite pattern (Table S2), which is compatible with the existence of competitive exclusion.

Some species, such as *E. penyalarense* and *J. crispa*, do not seem to be affected by competition with *F. curvifolia* canopies, probably because functional differences are greater, suggesting niche complementarity. *E. penyalarense* is a perennial species with deep axonomorph roots and woody-erectus stems with a maximum mean height over twice that of *F. curvifolia* stems (75.3 ± 29 mm and 32.4 ± 9.7 mm, respectively). *J. crispa* is a highly plastic and polymorphic species, loosely caespitose, with profusely branched stems and a prostrated-creeping growth. This allows individuals to find their way to available gaps in the clumps.

Interestingly, *F. curvifolia* cover (Fig. S3) did not explain the first-order heterogeneity in the distribution of the coexisting species (see results of the inhomogeneous Poisson processes). This heterogeneity may be related to some soil or microclimatic gradients or to some periglaciar processes involving snow cover and duration, which would affect the density and distribution of the coexisting species. These filters determine their coarse-scale distribution in the community and *F. curvifolia* patches control their fine-scale distribution. This also implies that the engineer and the coexisting species did not share the same microhabitat.

In contrast to the classical species to patch association approach, where species are only considered to be inside or outside the patch of a focal species, spatial pattern analyses of a complete community represent a conceptual advance that provides insights into the spatial scales where positive and negative associations are established. Our methodological approach and results show how a

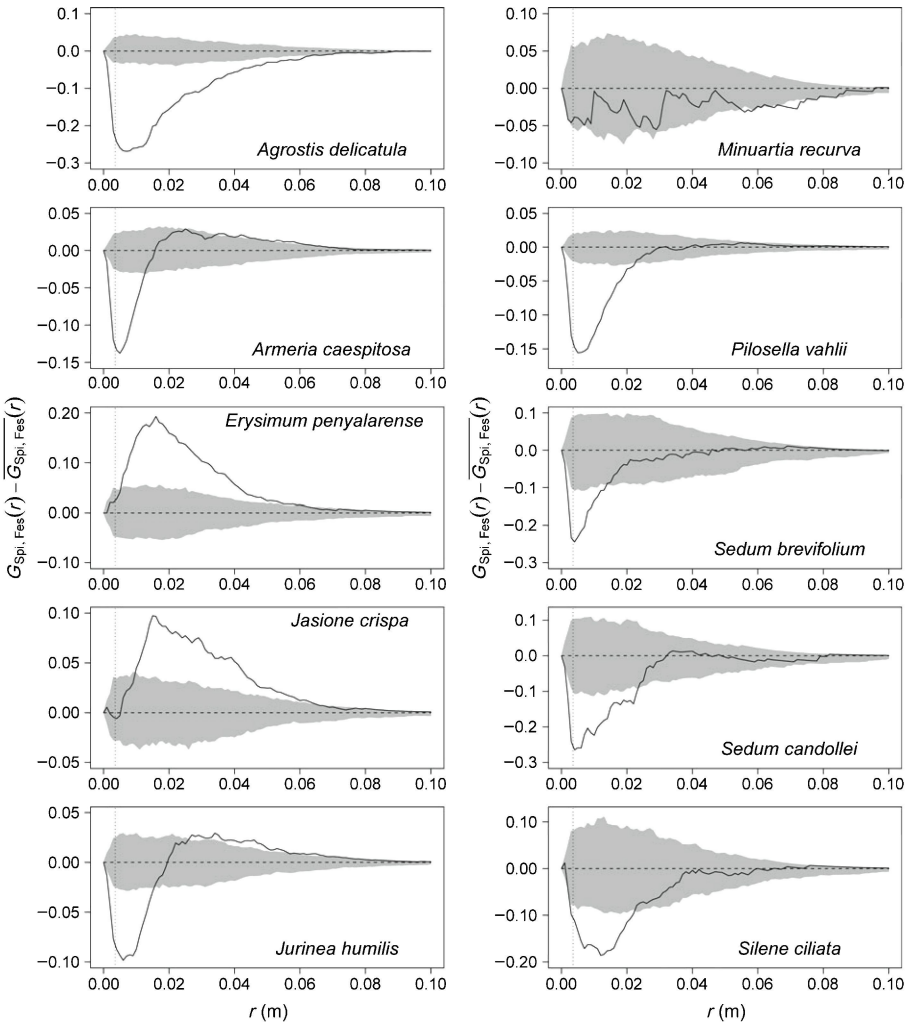

Fig. 1 Bivariate nearest-neighbor distance distributions from each coexisting species (Spi) to the nearest point of *Festuca curvifolia* masses of points. The *y*-axis represents the difference between the $G_{Spi,\,Fes}(r)$ observed (black line) and the mean value of 199 $G_{Spi,\,Fes}(r)$ functions computed on the same number of simulated bivariate patterns. Simulated bivariate patterns were built keeping the *F. curvifolia* point mass pattern 'fixed' and simulating each species with the best adjusted model. The fifth-lowest and fifth-highest values of simulations conform to the envelopes (grey area). Outside the envelopes, positive and negative values along the *y*-axis represent significant species association and dissociation, respectively.

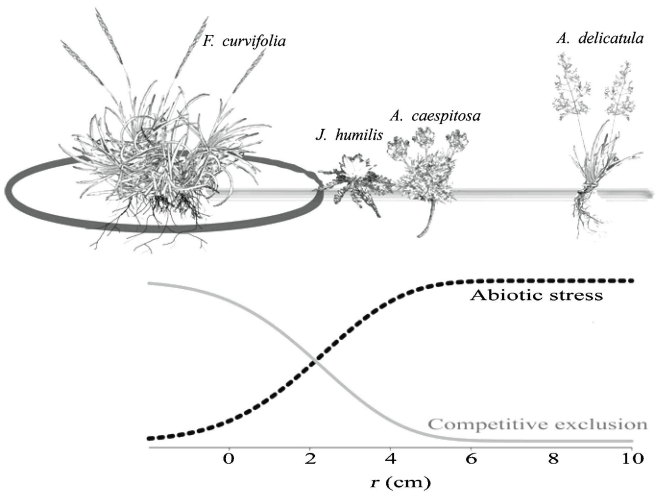

Fig. 2 'Facilitation in the halo' mechanism: a hypothesis for the spatial signal found at short and medium distances around *Festuca curvifolia*. Some coexisting species tend to occur close to the *F. curvifolia* halo where two opposite forces reach equilibrium: competitive exclusion by the *F. curvifolia* canopy (grey line) vs environmental severity of bare ground areas (black dashed line). Refer to Table 1 for full Latin binomials.

single species may act as an ecosystem engineer that influences the distribution and abundance of the coexisting species in the community. Furthermore, the range and the sign of this influence are mediated by the morphological and functional attributes of each species. *F. curvifolia* affected the realized patterns of the majority of the species in the community at small scales, promoting what we call the 'facilitation in the halo' mechanism. This mechanism induced a detectable spatial signature in most of the coexisting species, which tend to occur in an interphase zone where two opposite forces reach equilibrium: attenuated severe conditions as a result of proximity to an island of fertility and competitive exclusion mitigated by avoiding the *F. curvifolia* canopy.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Picture of the study site.

Fig. S2 Mark-correlation function of the size of the *F. curvifolia* pattern.

Fig. S3 Inhomogeneous L functions of each coexisting species adjusted to the *F. curvifolia* cover map.

Table S1 Best spatial model for each coexisting species

Table S2 Best models between distance to the nearest *F. curvifolia* patch and size of individual of each coexisting species